

Phytochemicals in Fruit and Vegetables: Health Promotion and Postharvest Elicitors

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Inverse associations between fruit and vegetable intake and chronic diseases, such as different types of cancer and cardiovascular disease, have been demonstrated in numerous epidemiological studies. Phytochemicals have been indicated to be responsible for this observed protective effect. Application of postharvest elicitors can trigger distinct changes in the plant's secondary metabolism. Thus, targeted postharvest elicitor treatments may be used to ob-

tain fruit and vegetables enriched with phytochemicals for sale as fresh market products or used as raw material for functional foods and supplements, thereby promoting higher consumption of these health-promoting substances.

Keywords signaling molecules, temperature, heat treatment, UV treatment, gamma irradiation, gas composition, ripening stage

I. INTRODUCTION

Due to the high and increasing incidents of cancer and heart disease in industrialized countries, governments have been

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making concerted efforts to raise public awareness about the advantages of eating a healthy diet (Erbersdobler, 2003). Overall, the primary prevention approach is aimed at reducing the estimated one third of cancer cases and up to one-half of cardiovascular disease cases that are thought to be diet related (Goldberg, 1994). Indeed, numerous epidemiological studies have already documented an inverse association between fruit and vegetable consumption and chronic diseases, such as different types of cancer and cardiovascular disease (e.g., Hirayama, 1990; Block *et al.*, 1992; Howe *et al.*, 1992; Steinmetz and Potter, 1991, 1996; World Cancer Research Fund/American Institute of Cancer Research, 1997; Joshipura *et al.*, 2001; Bazzano *et al.*, 2002; Kris-Etherton *et al.*, 2002). The plant compounds that are responsible for producing this health-promoting effect are the phytochemicals, which are present in the fruit and vegetables that we consume (Hauner and Watzl, 2001; Watzl, 2001).

However, the overall fruit and vegetable consumption in the industrialized nations of Northern Europe and North America is relatively low (Naska *et al.*, 2000; Agudo *et al.*, 2002; USDA, 2002), and is also well under internationally recommended amounts, i.e., approximately 250 g fruit and 375 g vegetables per day as advocated by many international health bodies (e.g., the World Cancer Research Fund/American Institute for Cancer Research, the Health Education Authority (UK), the German Nutrition Society, and the German Cancer Society). The reason for this low fruit and vegetable consumption may be designed suboptimally and led diet campaigns in which the message either did not get across or was misinterpreted. This could also be compounded by consumer complacency, low income, and poor educational standards (Naska *et al.*, 2000; Karg, 2004). Therefore, one way of increasing the consumption of health-promoting phytochemicals in the diet would be by increasing their levels in the fruit and vegetables themselves. Erbersdobler (2003) and Boeing *et al.* (2004) have already recommended such a dietary strategy for which they advocate the intake of functional foods that are enriched with phytochemicals in conjunction with low alcohol intake and fat consumption.

Recently, a number of specific crop production practices have been reported to enhance phytochemical content and composition in many fruit and vegetables crops such as *Vaccinium* spp. fruit and *Brassica* vegetables (Eichholz *et al.*, 2005; Schreiner, 2005). Moreover, specific postharvest elicitor treatments, such as low or high temperature treatments, ultraviolet and gamma irradiation, altered gas composition or application of signaling molecules, may further enhance phytochemical content.

Therefore, aims of this review are the following: (1) to present an overview of the types and effects of postharvest elicitor application on phytochemical content and composition in fruit and vegetables and (2) to discuss the implications of this in terms of targeted postharvest management.

A. Nature and Occurrence of Phytochemicals

Phytochemicals are grouped accordingly to their chemical structures and physiological functions and include carotenoids,

phenolic compounds, glucosinolates, saponins, sulfides, phytosterols, phytoestrogens, monoterpenes and protease inhibitors (Watzl and Leitzmann, 1999). Phytochemicals mediate the interaction of plants with their environment functioning as feeding deterrents, pollination attractants, and protective compounds against pathogens or various abiotic stresses, antioxidants or signaling molecules. Phytochemicals, such as polyphenols and carotenoids, are present in a wide range of fruit and vegetable crops, whereas some phytochemicals are distributed only among limited taxonomic groups. For example, glucosinolates are only found in the cruciferous vegetables crops, whereas the occurrence of sulfides is restricted to the Liliaceae. Additionally, each fruit and vegetable species has a distinct profile of phytochemicals, which is also within a special phytochemical group.

B. Nutritional Physiology of Phytochemicals

Fresh fruit and vegetables are naturally rich in phytochemicals (Rechkemmer, 2001). Phytochemicals reveal health promoting impacts as antioxidants, blood pressure or blood sugar influencing substances, or agents with anticarcinogenic, immunity-supporting, antibacterial, antifungal, antiviral, cholesterol-lowering, antithrombotic or anti-inflammatory effects (Watzl and Leitzmann, 1999). Groups of these functional compounds can consist of a wide range of substances. For example, antioxidative phytochemicals are carotenoids, phenolic compounds, protease inhibitors, sulfides, and phytoestrogens (Duyn and Pivonka, 2000; Tomas-Barberan and Espin, 2001). Some of these phytochemicals, such as phenolic compounds and sulfides, are marked by a broad spectrum of health-promoting functions (Watzl and Rechkemmer, 2001a, 2001b; Watzl, 2002).

C. Evidence for an Association Between Fruit and Vegetable Consumption and Chronic Diseases

Among food products, fruit and vegetables are especially known to have a high potential for preventing incidence of cancer and cardiovascular disease due to their broad range of health-promoting phytochemicals. Numerous epidemiological studies, conducted as prospective cohort or retrospective case-control studies and summarized by meta-analysis, concluded that a higher consumption of vegetables and fruit is associated consistently (but not universally for all cancer types) with a reduced risk of cancer. Fundamental meta-analyses in this field were done by Steinmetz and Potter (1991, 1996) and Block *et al.* (1992). Based on a 196 case-control and 21 cohort studies comprising meta-analysis, the World Cancer Research Fund/American Institute for Cancer Research (1997) provided convincing evidence for the inverse association between fruit and vegetable consumption and cancer risk. A protective effect of vegetable and fruit consumption against cancer was evident in 80 and 64 percent of the epidemiological studies, respectively.

However, for studies on special cancer types, the data are often contradictory. A meta-analysis of 26 prospective and retrospective studies by Gandini *et al.* (2000) confirmed the risk

reduction of breast cancer with enhanced intake of fruit and vegetables; whereas, in contrast, a pooled analysis of eight prospective studies indicated that fruit and vegetable consumption did not significantly reduce the risk to breast cancer (Smith-Warner *et al.*, 2001). Shannon *et al.* (2003) found a protective effect of vegetable and fruit intake at the highest quartile of consumption, suggesting a threshold effect in reducing breast cancer risk. However, the latest results of the Europe-wide prospective EPIC study (European Prospective Investigation into Cancer and Nutrition) with 285,526 women have demonstrated that a daily intake of 370 g fruit or 246 g vegetables is not associated with a reduced breast cancer risk (van Gils *et al.*, 2005).

Three large cohort studies by the Health Professional Follow-up Study (HPFS, $n = 88,764$), the Nurses' Health Study (NHS, $n = 47,325$) (Michels *et al.*, 2000) and one the Netherlands Cohort Study on Diet and Cancer ($n = 120,852$) (Voorrips *et al.*, 2000) showed no appreciable association between both fruit and vegetable intake and colon and rectal cancer. However, there was one exception in the Netherlands Cohort Study for colon cancer. Among women, an inverse association was observed between the total fruit and vegetable intake; however, only cruciferous vegetables and leafy vegetables showed a significant association. Recent studies have shown a distinct inverse association between vegetable and fruit consumption and colorectal cancer ($RR = 0.73$) (Terry *et al.*, 2001) and colon cancer ($RR = 0.50$) (Giovannucci, 2003). The data of both the HPFS and NHS have already been critically discussed since what was counted as "high end consumption" of vegetables and fruit was not particularly high (Flood and Schatzkin, 2000). Only 2% of participants in the NHS survey consumed more than 4.5 servings of vegetable per day; in the HPFS survey, only 3% had more than 3.5 vegetable servings per day. Therefore, due to the low percentage of participants consuming a high daily fruit or vegetable intake; the NHS survey could not prove that high fruit and vegetable consumption influence colon and rectal cancer risk.

Epidemiological studies also revealed distinct associations between cancer risk and certain vegetable or fruit families or categories, even though no associations were found between the total vegetable and fruit intake and cancer (Steinmetz and Potter, 1996; Voorrips *et al.*, 2000). For example, a high consumption of tomato or tomato-based products is consistently associated with a lower risk ($RR \leq 0.60$) of different cancer types as shown by a meta-analysis (Giovannucci, 1999), with the highest evidence being found for lung, prostate and stomach cancer. Tomato fruit are a rich source of carotenoids, especially lycopene and β -carotene. The epidemiological evidence suggested an inverse association of cancer with β -carotene either through diet or supplementation. Several β -carotene supplements given to heavy smokers have shown positive effects on lung cancer as the Alpha-Tocopherol, Beta-Carotene (ATBC) cancer prevention study ($n = 29,133$) (Heinonen and Albanes, 1994) and the β -Carotene Retinol Efficiency Trial (CARET) ($n = 18,314$) (Omenn *et al.*, 1996a) demonstrated. However, unexpectedly, after 18 months of supplementation at ATBC and 21 months

at CARET, an increased lung cancer risk was observed. Therefore, other carotenoids such as lycopene and α -carotene or a combination of carotenoids may have more potential in lung cancer prevention (Cooper *et al.*, 1999; Holick *et al.*, 2002). In several studies, plasma carotenoid concentrations are negatively correlated with the risk of cancer and also cardiovascular disease (e.g., Eichholzer *et al.*, 1996; Wallström *et al.*, 2003). Intervention with carotenoid-rich spinach powder, tomato and carrot juice (Müller *et al.*, 1999), and vegetable and fruit extracts (Wise *et al.*, 1996), revealed significant changes in the corresponding plasma carotenoid concentrations; whereas, supplementation with isolated β -carotene showed only a weak correlation to the plasma β -carotene concentrations ($r^2 = 0.22$) (Holick *et al.*, 2002). A recent, renewed evaluation of the CARET data revealed that two specific botanical groups of vegetables (Brassicaceae) and fruit (Rosaceae) were associated with a reduction of lung cancer ($RR = 0.68$ and $RR = 0.63$, respectively) (Neuhouser *et al.*, 2003).

The discrepancy between fresh vegetables and fruit along with their derived products and isolated supplementation may be due to other phytochemicals in the matrix of vegetables, fruit and their derived food products as well as their interactions on health-protective effects (Burri, 1997). Additionally, many phytochemicals seem to have hormetic effects on human health that depend on their concentration, and thus on their level of consumption (Trewavas and Stewart, 2003). Phytochemicals produce dose-dependent effects with high levels been detrimental to health; therefore, a daily β -carotene dose of 20 or 30 mg—as partly supplied in the ATBC study and in the CARET study, respectively—has to be classified critically in respect to human health effects.

In regard to chronic diseases, numerous epidemiological studies have accumulating evidence that a diet rich in vegetables and fruit may protect against cardiovascular disease (Ness and Powles, 1997; Law and Morris, 1998; Ness *et al.*, 1999; Liu *et al.*, 2000, 2001; Joshipura *et al.*, 2001; Bazzano *et al.*, 2002). Results from the First National Health and Nutrition Examination Survey (NHANES I) Epidemiologic Follow-up Study ($n = 9,608$) documented a strong inverse relationship of vegetable and fruit intake to mortality from cardiovascular disease ($RR = 0.73$), comparing at least 3 servings of vegetables and fruit per day to less than 1 serving per day and adjusted by various confounders (Bazzano *et al.*, 2002). A similar relative risk for cardiovascular disease ($RR = 0.78$) has been reported by the Women's Health Study ($n = 39,876$). However, this relative risk was obtained comparing 4.1 servings of vegetables and fruit per day to 2.6 servings per day (Liu *et al.*, 2000). The relative risk could be minimized to a great extent ($RR = 0.69$) by enhancing the vegetable and fruit consumption by up to 10.2 servings per day. Additionally, the recently conducted Kuopio Ischaemic Heart Disease Risk Factor (KIHD) Study on 2,682 men in Finland has provided further evidence that high intake of vegetables and fruit correlates with a reduced risk of cardiovascular disease ($RR = 0.59$) (Rissanen *et al.*, 2003). According

to the Physicians' Health Study (PHS, $n = 22,071$), the inverse relationship between vegetable intake and cardiovascular disease was more evident with smokers ($RR = 0.40$) consuming at least 2.5 servings per day in comparison with less than 1 serving per day (Liu *et al.*, 2001). Furthermore, legumes seem to play a key role in human diet in preventing cardiovascular disease. Legume consumption was significantly and inversely associated with the cardiovascular disease and lowered the relative risk by about 11% (Bazzano *et al.*, 2001). Interestingly, as also found for cancer, several investigations such as CARET (Omenn *et al.*, 1996b), PHS (Hennekens *et al.*, 1996) and the Women's Health Study (WHS, $n = 39,876$) (Lee *et al.*, 1999) with pure β -carotene supplementation (30 mg and 50 mg β -carotene per day, respectively), had no depressive effect on cardiovascular disease risk.

Conflicting findings from epidemiological studies could be caused by the limited validity of case-control studies due to an enhanced distortion of the cancer risk estimation by selection and recall bias. Cohort studies are less susceptible to such bias as information is collected before a disease develops (Gaziano, 2000). Thus, prospective cohort studies are recommended as the standard study selection in the epidemiological field (Willet, 2000). Additionally, overestimation in self-reported details about the vegetable and fruit intake in the questionnaire could be a further area of discrepancy due to the participant's projection of what they know they should consume instead of the reality of their consumption. Additional reasons for insufficient, only limited valid experimental results might be due to inconsistencies in the vegetable and fruit classification, differences in the assessment and in the supplied amount of vegetable and fruit intake or the lack of adequate consideration and interpretation of confounders, e.g., smoking, alcohol consumption, body mass index, serum cholesterol level, and physical activity (World Cancer Research Fund/American Institute for Cancer Research, 1997; Eichholzer *et al.*, 2001; Dekker and Verkerk, 2003; Shannon *et al.*, 2003). Highly detailed food-frequency questionnaires and the identification of unbiased biomarkers as indicators of vegetable and fruit consumption would be helpful to reduce the measurement error. Plasma concentrations of carotenoids were discussed as biomarkers, but the relative high variation in serum response within a test group shows the limited use of serum carotenoid concentrations as unbiased markers of vegetable and fruit intake. For cardiovascular disease, biomarkers such as the oxidation resistance of LDL, are discussed. Generally, the use of biomarkers should allow a faster test system than in previous studies (Eichholzer *et al.*, 2001).

In contrast, intervention trials avoid known and unknown confounding factor; however, the interpretation of the results offer limited validity for the investigated population group, the provided dose, the duration of the experiment and the combination of constituents or food products consumed in the study (Gaziano, 2000; Eichholzer *et al.*, 2001). When using other biological test systems besides humans, such as animal models or *in vitro* cultured cell systems, these experiments are strictly considered to provide information on animal-specific phytochemical

effects or mechanisms of action, and that these results cannot be extrapolated to their potential effects on human health (Dillard and German, 2000).

II. EFFECTS OF POSTHARVEST ELICITORS ON PHYTOCHEMICALS IN FRUIT AND VEGETABLES

Recently, due to health awareness campaigns, the general public has become more interested in foods that support and promote health. This trend has resulted in consumers wanting products with high health-promoting compound content rather than having superior external quality attributes as was previously the case.

Therefore, to meet this shift in consumer needs, the use of postharvest elicitors that can promote the levels of phytochemicals in postharvest crops has become an area of key interest (Goldmann *et al.*, 1999; Huyskens-Keil and Schreiner, 2004). The major factors that positively affect phytochemical content in postharvest crops are reported below. Moreover, how these physical and chemical factors may elicit an effect on secondary plant metabolism as well as on the subsequent phytochemical content and composition is also discussed.

In the present review, postharvest elicitors are defined as physical or chemical elicitors, which may induce the synthesis of phytochemicals in plants. In respect to the chemical elicitors, special emphasis is placed upon salicylic acid, methyl jasmonate, and ethylene because these signaling molecules are dominating the secondary plant metabolism. Therefore, the references cited herein are not intended to be a complete list of all reports on elicitor applications in postharvest influencing phytochemicals.

A. Physical Elicitors

1. Low Temperature

Storage temperature has a distinct influence on the phytochemicals present during the ripening stage of the product. For example, carotenoid changes occurring during storage depend on the initial physiological stage of fruit and vegetables (Gross, 1991), i.e., there is an increase in carotenoid content with continuing maturation or a decrease with senescence and these changes can be promoted or suppressed by temperature. β -carotene content of tomatoes, for instance, was observed to increase during storage when fruit were still in the ripening process and this increase was more pronounced at higher temperatures of up to 25°C; whereas, in some sweet potato cultivars, no increase in β -carotene during storage occurred as the synthesis of carotenoids was already completed by the time of harvest (Watada, 1987). This combined maturity-temperature effect was also observed in pepino (Prono-Widayat *et al.*, 2003). Premature and mature pepino fruit stored at 18°C showed a stronger increase of β -carotene compared to those stored at 5°C; however, in ripe pepinos, β -carotene were unaffected by temperature. In the case of lycopene as reported for several fruit and vegetables, this phytochemical's content increases at a temperature of about 25°C, but no synthesis occurs above 30°C (Goodwin and Jamikorn, 1952; Wills *et al.*, 1998).

Moreover, contents of lycopene and β -carotene precursors—phytoene, phytofluene and ζ -carotene—were highest in tomatoes stored at 20°C when compared with those stored at 30°C (Hamauzu and Chachin, 1995). This indicates that the activity of the key enzymes catalyzing the synthesis of β -carotene and lycopene, phytoene synthase and phytoene desaturase, is mainly triggered at the maturation process and can be additionally influenced by temperature. For example, temperatures above 30°C limit carotenoid production (Goodwin and Jamikorn, 1952; Wills *et al.*, 1998). This phenomenon may be due to reduced levels of phytoene synthase as reported for tomatoes (Lurie *et al.*, 1996).

In addition, the effect of temperature on glucosinolate content and composition depends on the developmental stage of the product. For storage at 5°C, glucosinolate content in cabbage increased until the beginning of senescence, and thereafter decreased rapidly (Chong and Berard, 1983). Distinct glucosinolate decomposition also occurred in cold stored (4°C) broccoli when the broccoli heads started to deteriorate (Rangkadilok *et al.*, 2002). This effect might have been caused by the senescence-induced loss of the cell membrane integrity (Farnsworth, 2004), leading to enhanced myrosinase activity, and thus to decreased glucosinolate contents. Berries such as strawberries, blueberries, and raspberries stored at temperatures >15°C have higher anthocyanins and phenolics contents compared to those stored at lower temperatures (0 to 6°C) (Kalt *et al.*, 1999; Cordenunsi *et al.*, 2005). Furthermore, Wang and Stretch (2001) found the highest anthocyanin and phenolic contents in cranberries stored at 15°C. The accumulation of anthocyanins may be due to the formation of carbon skeletons from organic acids, through interconversion with carbohydrates, for the synthesis of phenolics, including anthocyanins (Kalt *et al.*, 1999). This hypothesis is supported by the reduced titratable acidity in berries during storage (Kalt *et al.*, 1999).

In contrast, in products that are not sensitive to chilling (like apples), the flavonoid content showed a significant increase at low temperatures (2°C) (Lattanzio, 2003). Also, low temperatures stimulated an increase of anthocyanins in different apple cultivars (Reay, 1999). In pears, low temperature increased the red color as well as the activity of both phenylalanine ammonia-lyase and flavonoid-3-O-glycosyltransferase in the blushed pear ‘Rosemarie’; whereas in contrast, phenolics and enzyme activity in the red pear ‘Bon Rouge’ showed only a slight response to low temperatures. These observations indicate an additional genetic effect (Steyn *et al.*, 2004). According to Lattanzio (2003), the postharvest metabolic changes of phenolic compounds are often coupled with the activity of phenylalanine ammonia-lyase as low temperature induces phenylalanine ammonia-lyase activity in plant tissue.

Low temperature reduces the changes in glucosinolates during storage. However, rising storage temperature leads to increasing glucosinolate levels. For example, rutabaga roots and broccoli stored at 10°C showed an increase in individual aliphatic glucosinolates (Hansen *et al.*, 1995; Shattuck *et al.*,

1999), whereas to preserve glucoraphanin levels in broccoli, cooling at 4°C is recommended (Rodrigues and Rosa, 1999).

In respect to phytoestrogens, the content of isoflavone in soybeans could be maintained at 4°C, while temperatures up to 20 and 30°C caused a distinct degradation of these phytoestrogens (Hou and Chang, 2002). However, isoflavones of some soybean cultivars are nearly unaffected by the storage temperature, suggesting a genotype influence (Kim *et al.*, 2005).

Sulfides are also affected by storage temperatures. At room temperature, there was no possibility to maintain the content of sulfides in leek due to their decomposition (Stephani and Baltes, 1991). Kim *et al.* (2002) reported that increasing temperatures reduced the antimicrobial activity of garlic, which is associated with a decrease in the sulfide content. This temperature effect implies that alliinase may be the most critical rate-determinant for preserving sulfides. Therefore, to promote fruit and vegetable phytochemical contents, storage temperature has to be adapted to the product’s physiology; however, optimal storage temperature also depends on the origin of the product and thus on its chilling threshold, its genotype, and on the phytochemical compound itself.

2. Heat Treatment

To guarantee food safety and to address food quality issues, European governmental bodies have placed strong emphasis on the development and improvement of a range of postharvest treatments from high temperature application and irradiation (Harpaz *et al.*, 2001; Tang *et al.*, 2003) to ozone (e.g., Liew and Prange, 1994) and nitric oxide gas treatments (e.g., Wills *et al.*, 2000). In general, these postharvest treatments are known to accelerate the synthesis of stress-response compounds preventing fruit and vegetables from postharvest deterioration. These stress-response compounds are also known to be bioactive and to have human health promoting properties. According to Forbes-Smith (1999), activation of defense mechanisms due to stress, such as heat or irradiation (e.g., UV-C light), can result in three main responses: (1) changes of structural barriers (phenolics, decomposition of lignin, waxes, suberin, etc.); (2) enhancement of constitutive inhibitors (antimicrobial compounds) and phytoalexins; and (3) activation of specific proteins (chitinases, glucanase, etc.). Interestingly, in *Brassica* vegetables, phytoalexins and indole glucosinolates, known to have cancer-preventive properties, have linked biosynthesis pathways as both are derived from the intermediate indole-3-acetaldoxime (Glawischnig *et al.*, 2004).

Heat treatment is one method that allows the reduction of postharvest quality loss and suppression of pathogen development by inducing modifications in the physiological and physicochemical processes of fruit and vegetables after harvest (Brodl, 1989). However, exposure of fresh commodities to heat also affects cellular protein synthesis leading to inactivation of enzymes related to quality loss, e.g., in texture and color (Lurie, 1998; Ben-Yehoshua, 2003). Moreover, heat treatment is known to promote activities of enzyme-mediated processes (e.g., catalase and polyamine synthesis in terms of

inducing chilling resistance), while inhibiting synthesis processes (e.g., 1-aminocyclopropane-1-carboxylic acid oxidase, glucanase, and chitinase proteins), thereby affecting various physiological events (Lurie, 1998; Fallik, 2004). Products can be heat treated in a variety of ways including hot water immersion as well as hot water rinsing and brushing (Fallik, 2004). The kind of application that would be best for the crop depends on physiological responses of cultivars of different fruit and vegetable species and these vary according to season, growing location, soil type, production practices, and stage of maturity.

In various fruit and vegetables (e.g., tomato, melon, mango), hot water treatment (at 35°C for 12 h, at 55°C for 5 min and 42°C for 24 h, respectively) is reported to inhibit polyphenol oxidase and peroxidase activities leading to delayed anthocyanin synthesis, and thus protection of color pigment changes by maintaining the anthocyanins in their red-pigmented form with high antioxidative activity in postharvest (Civello *et al.*, 2001; Harpaz *et al.*, 2001; Fallik, 2004). A possible activation of the antioxidative system is suggested by the further induced superoxide dismutase activity and suppression of peroxidase activity following heat treatment of sweet basil and papaya (Faure-Mlynkski *et al.*, 2005; Huajaikaew *et al.*, 2005). Moreover, hot water treatment has been found to be effective in delaying carotenoid synthesis and thus yellowing of broccoli florets (at 40°C for 60 min) and kale (at 45°C for 30 min), while it did not affect brussels sprouts (Wang, 2000). High temperature treatment also suppressed 1-aminocyclopropane-1-carboxylic acid oxidase activity and thus indirectly prevented carotenoid synthesis (Suzuki *et al.*, 2005). Additionally, specific genes encoding ethylene biosynthesis are assumed to be inhibited by heat treatment. Furthermore, hot air treatment (at 48°C for 3 h) of broccoli florets delayed the onset of chlorophyll *a* degradation by reducing the activity of chlorophyllase, Mg-dechelatase, and peroxidase (Costa *et al.*, 2005). Moreover, the breakdown of ascorbic acid in broccoli heads was retarded by hot water treatment prior to storage (Kazami *et al.*, 1991).

In lemon fruit, hot water dipping (55°C for 20 sec) resulted in rapid production of a lignin-like material, followed by accumulation of the phytoalexins scorparone and scopolitin (Ben-Yehoshua *et al.*, 2000; Nafussi *et al.*, 2001). In contrast, in pomegranate, hot water treatment (35 or 45°C for 2 or 5 min, respectively) did not affect ascorbic acid content although a reduction of chilling sensitivity was observed (Mirdehghan and Rahemi, 2005). Similar results were found in 'Clementine' mandarins where ascorbic acid and carotenoid contents were not affected by heat treatments (Erkan *et al.*, 2004).

Numerous reports have shown that high temperature application as well as ozone and nitric oxide gas treatments are very effective in decay control, enhancing fruit resistance to chilling injury as well as delaying ripening processes. However, information about the beneficial effects on health-promoting phytochemicals in fruit and vegetables during postharvest are scanty and has to be investigated in more detail.

3. Ultraviolet and Gamma Irradiation

Ultraviolet irradiation acts as an abiotic physical elicitor of resistance mechanisms, and thus leads to a rapid increase of stress-response compounds such as phenols, flavonoids, and phytoalexins (Oufedjikh *et al.*, 2000; Higashio *et al.*, 2001; Ben-Yehoshua, 2003). Gamma and ultraviolet irradiation extend the shelf life of fresh and processed fruit and vegetables by destroying food-borne pathogens, such as fungi and bacteria (e.g., *Salmonella* spp., *Listeria monocytogenes*, *Staphylococcus aureus*), and insects (Snowdon, 1991; Marquenie *et al.*, 2002; Mitcham *et al.*, 2005). Irradiation is also applied to various tropical and subtropical products, e.g., papaya, avocado, banana, lychee, and oranges in order to suppress microbiological decay causing severe losses during long distance oversea transport (Snowdon, 1991). Moreover, UV-C treatment (3.7 kJ m⁻²) is known to especially retard ripening and senescence processes (Liu *et al.*, 1993; Maharaj *et al.*, 1999). However, the exact mode of action of UV treatment still has to be investigated in more detail.

The biosynthesis of phenolic compounds is affected by gamma and ultraviolet irradiation due to the increased activity of phenylalanine ammonia-lyase. This effect was found in several fruit and vegetables such as citrus (Oufedjikh *et al.*, 2000), apples (Dong *et al.*, 1995), peas (Pluskota *et al.*, 2005), and witloof chicory (Hanotel *et al.*, 1995). The increased phenylalanine ammonia-lyase activity promotes the biosynthesis of phenolic compounds, for example, flavanones in citrus spp. (Oufedjikh *et al.*, 2000), anthocyanins in peach (Kataoka and Beppu, 2004), and resveratrol in grapes (Takayanagi *et al.*, 2004); however, an undesired browning can also occur due to the formation of melanines in pomegranates and rockmelons (McDonald *et al.*, 2000, 2005). This diametric effect is assumedly due to the different applied doses of irradiation that commonly vary between 0.2 and 8 kJ m⁻² (Terry and Joyce, 2004).

In addition to phenylalanine ammonia-lyase induction, ultraviolet irradiation increases the activity of other enzymes involved in flavonoid synthesis: chalcon synthase, chalcon isomerase, and dihydroflavonol-4-reductase (Tomas-Barberan and Espin, 2001). However, UV-B irradiation (UV-B + incandescent light) had no effect on anthocyanins in apples and pears (Marais *et al.*, 2001a).

Flavonoids have various physiological functions such as antioxidative or antitumor activity as well as a UV protective effect (Higashio *et al.*, 2001). UV irradiation (UV fluorescent lamp, 310 nm, 20 w) of spinach leaves was observed to result in an increase of α-tochopherol and quercetin contents. Also, in strawberry and onions, anthocyanins and quercetin were found to be promoted by UV irradiation (254 nm, 310 nm, and 352 nm at doses between 71–1294 μW cm⁻²) after harvest (Higashio *et al.*, 2005).

UV-C (254 nm, 3.7 KJ m⁻²) and chitosane have also been reported to activate plant defense mechanisms, e.g., the acceleration of phenolic compounds and accumulation of phytoalexins (rishitin) in tomato (El-Ghaouth *et al.*, 1992; Stevens

et al., 1996; Charles *et al.*, 2003, 2005). However, the responsiveness of harvested horticultural produce to UV-C treatment declines with increasing fruit ripening, and thus depends on the harvest time (Terry and Joyce, 2004). Similar results were reported for grapefruits treated with gamma irradiation (Patil *et al.*, 2004). Low doses (≤ 200 Gy) of irradiation are recommended for enhancing health-promoting compounds (e.g., flavanones, β -carotene, lycopene, and ascorbic acid content) in early season grapefruit, while higher doses (400–700 Gy) showed detrimental effects. No effect was observed on the quality of late season fruits.

Moreover, gamma irradiation (60 kGy) was found to change membrane permeability of garlic, favoring water loss in the clove protective leaves and thereby preventing weight loss of the bulb (Pellegrini *et al.*, 2001). Changes in the state and localization of anthocyanins are assumed to be related to the water content. Increase in oxidative-free radicals produced by dehydration during postharvest could therefore decrease the intracellular pH, favoring oxidative processes such as synthesis of anthocyanins and decomposition of lignin. In contrast, no effect of gamma irradiation (0.5–1 kGy) on nutritional parameters (carotenoid, vitamin C) was found in apricots, although enzymes of the antioxidant system such as peroxidase increased significantly (Egea *et al.*, 2005). Finally, postharvest irradiation with a high-pressure sodium light in combination with low temperatures, (i.e., 120 h at 6°C) increased anthocyanin synthesis of 'Cripps Pink' apples during storage (Marais *et al.*, 2001b).

In conclusion, how the different types of irradiation affect the physiology of the plant is still unclear and more studies are needed for a better understanding of both the biological basis of defense mechanisms leading to induced resistance as well as the promotion of stress-response compounds and the process of retardation of ripening.

4. Altered Gas Composition

In general, in controlled atmosphere (CA) storage and modified atmosphere packaging (MAP), oxygen concentration is reduced and carbon dioxide concentration increases in the ambient atmosphere of the product. These changes in gas composition influence the phytochemical content in fruit and vegetables.

Radishes packed in modified atmosphere (8.3 kPa O₂ + 5.4 kPa CO₂) showed an accumulation of glucosinolates after 5 days of storage (Schreiner *et al.*, 2003). Also, the glucosinolate content of broccoli stored in a controlled atmosphere (0.5 kPa O₂ + 20 kPa CO₂) increased continuously during 7 days of storage (Hansen *et al.*, 1995). Hansen *et al.* (1995) proposed that this increase in glucosinolate content could be associated with a de novo glucosinolate biosynthesis based on metabolites (e.g., amino acids) originating from the decomposition of other compounds. This process also seems to take place in radish packed in a modified atmosphere (Schreiner *et al.*, 2003). Presumably, the glucosinolate increase in controlled and modified atmospheres is a stress response of the product to the increased CO₂ and decreased O₂ concentrations. The hypothesis of stress-

induced accumulation of glucosinolates is supported by Verkerk *et al.* (2001). They detected increased levels of indole glucosinolates after chopping and storage of cabbage and broccoli under ambient conditions, indicating a stress response on mechanical impact. Finally, postharvest stress due to altered gas composition led to an increased saponin content in modified-atmosphere packed asparagus spears (Schwarzbach, 2004).

Changes in cell pH by altered gas composition affect the anthocyanin content since the vacuolar acidity influences the formation of the various anthocyanin forms. In the acid pH range, anthocyanins are predominantly present as red flavylium cation, and with rising pH mainly the colorless carbinol and the blue quinonoidal bases are synthesized leading to a scarlet color (Herrmann, 1991). In strawberries, high CO₂ concentrations (20 kPa) increased the pH due to the enhanced decomposition of organic acids (Halcroft and Kader, 1999). The degradation of organic acids in altered gas conditions was also found in lettuce (Darezzo *et al.*, 2003) and fennel (Escalona *et al.*, 2003). Changes in anthocyanins correlated closely with color changes in strawberries leading to a scarlet coloring (Halcroft and Kader, 1999). Similar effects were documented for radish stored in modified atmosphere (Huyskens-Keil and Schreiner, 2003). In pomegranates, Holcroft *et al.* (1998) also found reduced anthocyanin levels with rising CO₂ concentrations (10 and 20 kPa), which were correlated with decreased phenylalanine ammonia-lyase activity. This indicates a suppression of anthocyanins biosynthesis by elevated CO₂ concentrations.

Not only continuous, but also varying atmosphere conditions during storage, where either O₂ or CO₂ is changed for a short period with subsequent return to the initial concentration set point, could maintain phytochemical content as demonstrated for pepino fruit (Huyskens-Keil *et al.*, 2005). CA storage of mature pepino fruit for a total of 21 days with varying high CO₂ concentrations (15 kPa for 2 days followed by 5 kPa for 19 days) maintained significantly the chlorophyll and tentatively the β -carotene content. In contrast, high continuous CO₂ concentrations (15 kPa) caused a strong reduction of chlorophyll and β -carotene within 14 days. This CO₂ sensitivity of chlorophyll was also found in broccoli, lettuce, and cucumber (Kader, 2002; Saltveit, 2003) and in spinach, melon, and kale for β -carotene (Kader, 2002).

Very little information is available on the effects of elevated O₂ concentrations on phytochemicals. Day *et al.* (1998) reported that high O₂ levels did not decrease the level of antioxidants in fresh-cut lettuce compared with low O₂ levels. Finally, lycopene synthesis in *rin* tomatoes was enhanced in fruit stored at 60 or 100 kPa O₂ in the presence of ethylene (Frenkel and Garrison, 1976).

B. Chemical Elicitors

The effects of chemicals applied to harvested fruit and vegetables were investigated mainly in respect to sensory properties, such as color or firmness loss, or changes in organic acids and carbohydrates. Currently, only limited information is

available on the effects on phytochemical content due to postharvest chemical elicitor application.

Salicylic acid, methyl jasmonate, and ethylene serve as signaling molecules induced by pathogen infestation (Zhao *et al.*, 2005) and mechanical wounding (Bondaryk, 1994). These elicitors trigger signal cascades that activate several defense responses such as the synthesis of phytochemicals, e.g., glucosinolates (Mikkelsen *et al.*, 2000), polyphenols (Cisneros-Zevallos, 2003), or saponins (Xu *et al.*, 2005).

1. Methyl Jasmonate and Salicylic Acid

Methyl jasmonate induces anthocyanin biosynthesis by induction of chalcon synthase and dihydroflavonol-4-reductase gene expression (Tamari *et al.*, 1995; Saniewski *et al.*, 1998). Therefore, after postharvest methyl jasmonate application, increased anthocyanin contents and antioxidant activities (phenolics and ascorbic acid) were observed in apple (Rudell *et al.*, 2002), potatoes (Reyes and Cisneros-Zevallo, 2003) as well as in guava, mango, banana, and papaya (Kondo *et al.*, 2005). Application of methyl jasmonate also enhanced the activity of phenylalanine ammonia-lyase and thus the content of other flavonoids (Tomas-Barberan and Espin, 2001; Gonzalez-Aguilar *et al.*, 2004). As demonstrated in carrot callus culture, salicylic acid also stimulates anthocyanin biosynthesis (Sudha and Ravishankar, 2003). Moreover, methyl jasmonate promotes β -carotene biosynthesis in tomato (Saniewski and Czapski, 1983) and in apple (Perez *et al.*, 1993). This effect could be caused by direct stimulation of β -carotene or by an indirect enhancement of the β -carotene biosynthesis via promotion of ethylene by methyl jasmonate (Perez *et al.*, 1993). Methyl jasmonate and salicylic acid treatments on Chinese oilseed rape breeding lines produced an increase in leaf indole and aromatic glucosinolates respectively. However, the extent of such increases differed widely between the lines (Li *et al.*, 1999).

2. Ethylene

Ethylene triggers the ripening and senescence of fruit and vegetables, and hence could promote the content of phytochemicals in postharvest (Kader, 2002). Postharvest ethylene treatment of pre-climacteric fruit or fruit vegetables, such as banana or tomato, increases the synthesis of carotenoids (Wills *et al.*, 1998). As demonstrated in apricot fruit, ethylene treatment is associated with carotenogenic gene expression and the corresponding carotenoid accumulation (Marty *et al.*, 2005).

In contrast, in non-climacteric fruit and vegetables, ethylene mainly induced an enhanced senescence associated with a fast decomposition of primary and secondary metabolites (Kader, 2000), or as in the case of bell pepper, no significant differences were noted for carotenoids and phenolics due to postharvest ethylene exposure (Fox *et al.*, 2005).

Moreover, ethylene treatment of grape berries was associated with an increase in gene expression of chalcon synthase, flavanone 3-hydroxylase, leucoanthocyanidin dioxygenase, and UDP glucose-flavonoid 3-O-glucosyl transferase leading to en-

hanced anthocyanin synthesis (El-Kereamy *et al.*, 2003). Thus, ethylene affects partly the same enzymes in the anthocyanin biosynthesis as methyl jasmonate; thus, reflecting multiple signaling pathways of chemical elicitors (Zhao *et al.*, 2005). However, as shown in apples, other phenolics compounds such as flavonoids and chlorogenic acid were not affected by ethylene treatment (Awad and de Jager, 2002), suggesting a specific ethylene susceptibility of anthocyanin biosynthesis.

In contrast to methyl jasmonate and salicylic acid, ethylene application influences saponin and terpene content. In ginseng, the induction of 1-aminocyclopropane-1-carboxylic acid oxidase led to an ethylene release and increase of saponin synthesis, which was indicated by increased mRNA expression of squalene synthase, squalene epoxidase, and beta-amyrin synthase (Xu *et al.*, 2005). Ethylene treatment of carrots also caused an increase of terpenes, particularly terpinene, limonene, and caryophyllene, but led to a bitter and terpene-like taste (Seljasen *et al.*, 2001).

III. FUTURE PROSPECTIVES

To date, the effectiveness of postharvest treatments has been assessed mainly by the quality maintenance of harvested fruit and vegetables. However, with rising consumer interest in foods that promote health, attention has shifted from quality maintenance to quality assurance with particular emphasis on the enhancement of health-promoting phytochemicals. Therefore, to obtain fruit and vegetables enriched with phytochemicals, postharvest elicitor treatments might be used either singularly or in combination to elicit the desired effect. To ensure an efficient and consumer-oriented supply chain, these postharvest elicitor treatments should be coordinated with crop management strategies. Such phytochemical-enriched fruit and vegetables could be served as fresh products or used as raw material for functional foods and supplements and would act as a complementary or synergistic strategy to human nutrition programs and nutrition policy for enhancing the consumption of phytochemicals.

However, investigations on the beneficial effects of physical and chemical postharvest elicitor treatments on health-promoting phytochemicals in fruit and vegetables have to be extended. Plant response in terms of physiological, biochemical, and molecular biological processes have to be studied in more detail for the optimization of elicitor application.

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